

THE CONIFERS *FRENELOPSIS* AND *MANICA* IN THE CRETACEOUS OF PORTUGAL

by K. L. ALVIN

ABSTRACT. *Frenelopsis* Schenk has been used to accommodate various species of fossil conifers with segmented shoots and small scale-like leaves at the nodes. As a contribution to the revision of conifers of this type, some of which probably have an affinity with *Hirmeriella* Hörhammer, the species from the Cretaceous of Portugal are here redescribed. Four species are now recognized: three (one tentatively) are retained in *Frenelopsis*, while the fourth, with spirally instead of cyclically arranged leaves, is placed in *Manica* Watson.

THE genus *Frenelopsis* was erected by Schenk (1869) for some segmented conifer shoots, somewhat resembling those of the modern genus *Callitris*. Schenk identified his specimens which were from the Cretaceous of the Carpathians as belonging to the same species as those earlier described by Ettingshausen (1852) from the Cretaceous of Austria as *Thuites hoheneggeri*. Since then *F. hoheneggeri* has been reported from various parts of the world and some ten other specific names have been erected. Unfortunately, the genus defined only on the basis of the brief descriptions and drawings in these early publications, has been used to accommodate quite a wide range of species. Recent efforts by a number of palaeobotanists to locate Schenk's and Ettingshausen's original material have so far been fruitless.

An important character of the type material which is uncertain is the leaf arrangement. Some parts of the specimens illustrated in Ettingshausen's paper appear to show leaves in cyclic arrangement with three or four at each node. Schenk describes the leaf arrangement as opposite decussate, but the only illustration that shows it (Schenk, pl. 6, fig. 6) has the appearance of an interpretative diagram and not a drawing of a specimen. Another doubtful character in both Ettingshausen's and Schenk's material is the presence or absence of suture lines or grooves running down the internode from the margins of the leaves above such as occur in modern Cupressaceae. Ettingshausen's figures show such lines, at least on the main axes. Of Schenk's figures, while some show somewhat coarse ridges and furrows, in none, except the small specimen shown in plate 6, fig. 5 which may represent a different conifer, do these look like suture lines. Most modern authors have assumed that the absence of suture lines is a generic character. However, Kon'no (1966) has described a species from Malaysia, *F. malaiana*, with opposite decussate leaves and well-defined suture lines; this I would include in *Cupressinocladus*.

Velenovsky (1888) described *F. bohémica* from the Upper Cretaceous (Cenomanian) of Czechoslovakia. He described it as leafless, but Němejc (1926) redescribing the species showed that the leaves were in whorls of three and that the internodes lacked sutures. Hlušík (1972, 1974) has shown that the correct name of this species is *F. alata* (K. Feistmantel) Knobloch.

Of the several other species which have been described, most have lacked suture lines. Leaf number and arrangement has frequently not been referred to, but in

some it has been shown to be only one per node, e.g. *F. parceramosa* Fontaine (1889).

Dr. Joan Watson, in the course of her revision of the English Wealden flora (unpublished thesis, University of Reading, 1964), encountered a conifer with segmented shoots and small spirally arranged leaves, one per node, which she tentatively identified with Fontaine's species. She has proposed that a new generic name *Manica* Watson (1974) should be used for species resembling *Frenelopsis* but with this different leaf arrangement.

Conifers of the *Frenelopsis* type occur mainly in the Cretaceous, though Barale (1973) has reported *F. rubiesensis* Barale, a species with leaves in whorls of three and no suture lines, from beds of Upper Jurassic age in Spain.

The first record from Portugal of a fossil conifer of the *Frenelopsis* type was by Heer (1881) who described some shoots from the Lower Cretaceous (Aptian-Albian) as a new species, *F. occidentalis*. The same name was used by Saporta (1894) for further specimens from Cercal (Barremian), Nazaré (Cenomanian), and Padrão (Cenomanian). He erected another species, *F. leptoclada* Saporta, for specimens from Caixarias (Aptian) and from San Sebastian, Spain (Valanginian). Lima (1900) recorded specimens which he referred to as *F. occidentalis* Heer from Esgueira (Senonian) but Teixeira (1946) referred these specimens to '*F. aff. hoheneggeri*'.

Romariz (1946) in a revision of the Portuguese *Frenelopsis* species recognized three species: *F. hoheneggeri* (Ettingshausen) from the Lower Cretaceous of Almagem and Olhos Amarelos in which specimens believed to be Heer's (1881) holotype of *F. occidentalis* were included, *F. lusitanica* Romariz from Nazaré (now regarded as Cenomanian), and *F. oligostomata* (Romariz) from the Senonian of Esgueira.

All the available material of *Frenelopsis* in the Museum of the Serviços Geológicos de Portugal has been re-examined. This material does not have catalogue numbers.

SYSTEMATIC DESCRIPTION

Order CONIFERALES

Family ?CHEIROLEPIDIACEAE

Both *Frenelopsis* and *Manica* are tentatively classified in this family on the basis of Hlušík and Konzalová's (1976) report of pollen of the *Classopollis* type in male cones attributed to *F. alata* and also similar pollen which Dr. Watson and I have found in male cones attributed to a *Manica parceramosa* (Fontaine) from the English Wealden.

Genus FRENELOPSIS Schenk

Frenelopsis alata (K. Feistmantel) Knobloch

Plate 41, figs. 1-5; Plate 42, figs. 1-6; text-fig. 1A

- 1881 *Sclerophyllum alatum* K. Feistmantel, p. 96; pl. 7, fig. 1a-k.
- 1882 ?*Frenelopsis hoheneggeri* (Ettingshausen): Zeiller, p. 231; pl. 11, figs. 1-10.
- 1888 *Frenelopsis bohémica* Velenovsky, p. 590; figs. 1, 2, 10.
- 1894 *Frenelopsis occidentalis* Heer: Saporta, p. 199; pl. 36, figs. 1, 2.
- 1921 *Frenelopsis bohémica* Velenovsky: Bayer, p. 41; text-figs. 5, 6.

- 1926 *Frenelopsis bohemica* Velenovsky: Němejc, p. 133; pl. 1, figs. 1-3; pl. 2, figs. 1-5; pl. 3, figs. 1-4.
1946 *Frenelopsis lusitanica* Romariz, p. 144; pl. 3, figs. 2, 3; pl. 4, figs. 1, 2.
1948 *Frenelopsis lusitanica* Romariz: Teixeira, p. 102; pl. 43, fig. 2, 2a.
1974 *Frenelopsis alata* (K. Feistmantel): Hlušík, pl. 1, figs. 3, 4; pl. 3, figs. 1, 2.
1975 ?*Frenelopsis* (from le Brouillard): Broutin and Pons, p. 10, pls. 1-4 (specimens from le Brouillard).

Locality. Nazaré, Estremadura, Portugal.

Horizon. Cenomanian.

Description. Four good specimens of this species exist in the Lisbon collection. The one figured by Romariz (pl. 4, fig. 2) and also by Teixeira was used in the present study of the cuticle. Some of the specimens are partially pyritized and somewhat decomposed, others are compressed and carbonized. These latter usually show more or less prominent longitudinal furrowing, probably produced by shrinkage at some stage, but the pyritized specimens have a smooth surface.

All the specimens show up to three orders of branching. The stoutest axes are up to 5 mm broad and have segments two to three times longer than broad; they are more or less straight and branched at nearly every node. Lateral branches have longer, narrower segments; these penultimate branches are up to 2 mm wide and somewhat zigzag due to an almost pseudodichotomous mode of branching. The ultimate branchlets, arising singly at almost every node on the penultimate, are about 1 mm wide, with segments many times longer than wide. Branches arise from parent shoots at about 30°, disregarding the zigzag.

There is no doubt that at least the ultimate branchlets had leaves in whorls of three. Plate 41, fig. 1a, b shows two sides of the same node of an ultimate branch. The leaves are triangular, about 0.6 mm wide, 0.3 mm long, and have a fringe of unicellular hairs along the margins (Pl. 41, fig. 4). The leaves are joined laterally to form a sheath as much as 1 mm deep. The form of the leaf-sheath on axes of lower orders is not clear, but its general appearance is similar.

The internode cuticle is about 30 μm in total thickness (measured in folds under the light microscope) with the outer periclinal epidermal wall about 8 μm . Sometimes the cuticle on one side of the specimen appears paler and thinner than that on the other; differences are also seen in the SEM view of the outer surface (cf. Pl. 42, figs. 1, 2). The darker more robust cuticle (represented in fig. 1) looks smooth at low magnification, but at high magnification shows some patterning (just discernible in the figure) suggestive of surface wax, whereas the cuticle from the opposite side (fig. 2) shows furrows marking the outlines of epidermal cells and is without evidence of wax. Whether these differences reflect a degree of dorsiventrality cannot be decided on present evidence. It is probably that side of the shoot which is uppermost and exposed on the block which has the thinner, paler type, and it is therefore possible that the exposed cuticle has suffered some kind of degradation since the specimens were collected. The very limited amount of material at my disposal has precluded any further investigation of this problem.

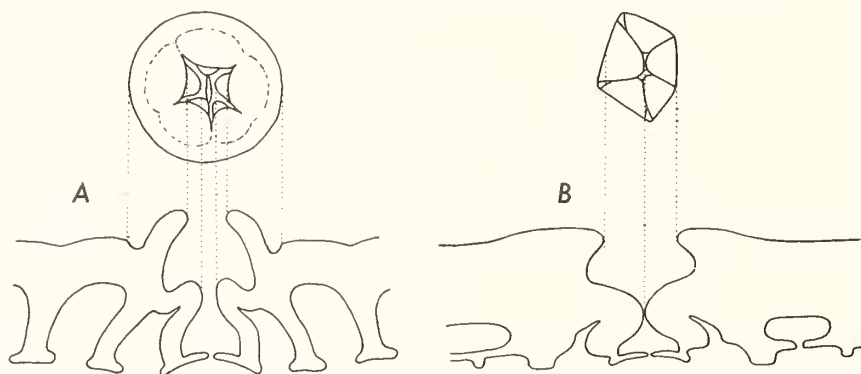
The epidermal cells are very clearly seen in both the light microscope and the SEM. They are rather uniform, mostly slightly elongated, but never more than twice as long as broad; longitudinal rows are fairly well marked, (20-) 25 (-45) μm wide. The anticlinal walls are about 4 μm thick. Though portions of the inner periclinal

walls of the epidermis may be cutinized (Pl. 42, figs. 3, 4), the hypodermis is generally not marked except in the region of the leaf and sheath (Pl. 42, fig. 6).

The stomata are optically denser than the rest of the cuticle and therefore conspicuous in the light microscope (Pl. 41, fig. 2). They are arranged in rather irregular longitudinal rows, the rows being spaced irregularly, with one to four epidermal cells between, and the stomata irregularly spaced (75–150 μm apart) in the rows (Pl. 41, figs. 2, 5).

Stomata continue up on to the base of the sheath but fade out on the teeth-like leaves themselves which were therefore presumably non-photosynthetic. Stomata continue abundantly towards the node below on that part covered by the lower sheath, only ceasing very close to the node.

The stomata are highly specialized, with four to five (or six) subsidiary cells surrounded by a ring of a usually greater number of somewhat specialized epidermal cells. The form of the stomatal pit is shown reconstructed in text-fig. 1A. This is



TEXT-FIG. 1. A, *Frenelopsis alata* (K. Feistmantel) Knobloch. Reconstruction of outside view of stoma and section of cuticle, $\times 500$. B, *?Frenelopsis occidentalis* Heer. Reconstruction of outside view of stoma and section of cuticle, $\times 500$ approx.

based on sections viewed in the SEM (Pl. 42, fig. 5) and also on surface views (Pl. 42, figs. 1, 2) and light microscope observations (Pl. 42, figs. 2, 3). The stomatal pit has a polygonal or more or less stellate mouth surrounded by a lobed canopy. The lobes are not always very distinct, but their number equals that of the subsidiary cells rather than that of the surrounding epidermal cells. I conclude, therefore, that they represent parts of the subsidiary cells. In the throat of the pit is a series of papillae again equal in number to the subsidiary cells. The guard-cell cuticles are thin and

EXPLANATION OF PLATE 41

Frenelopsis alata (K. Feistmantel) Knobloch, from Nazaré (Cenomanian).

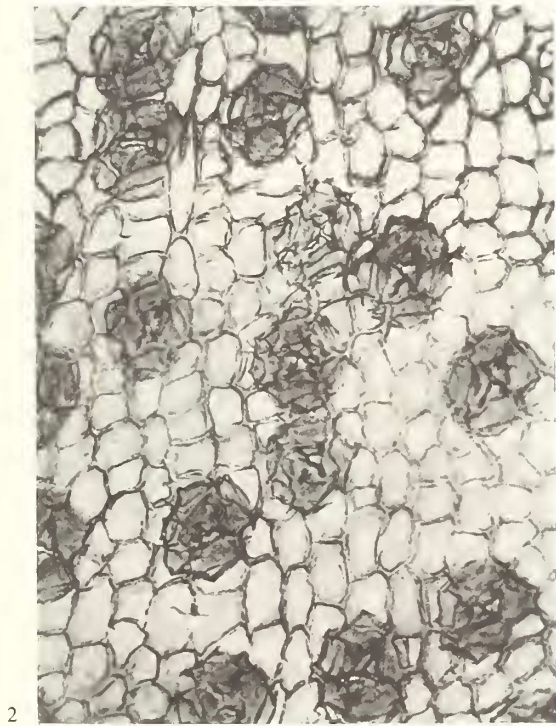
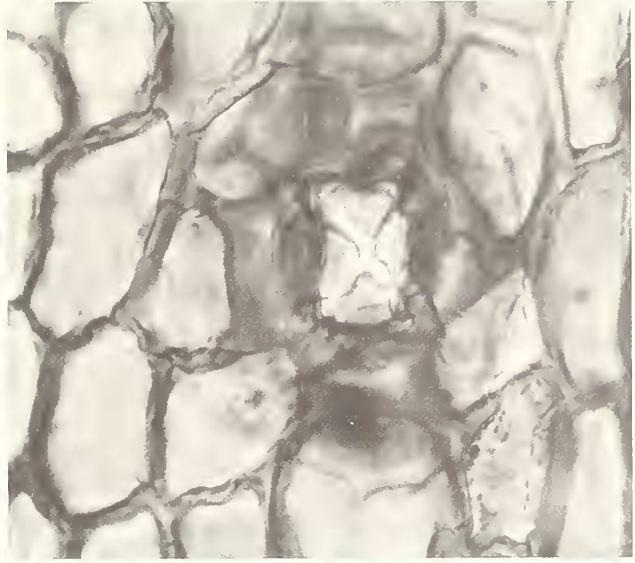
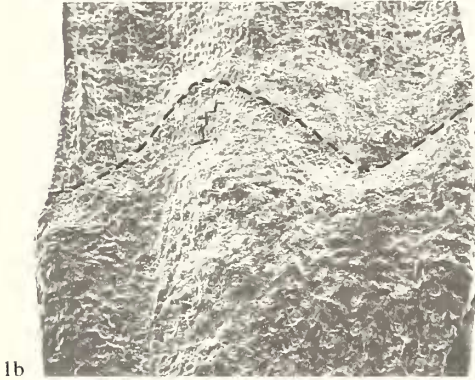
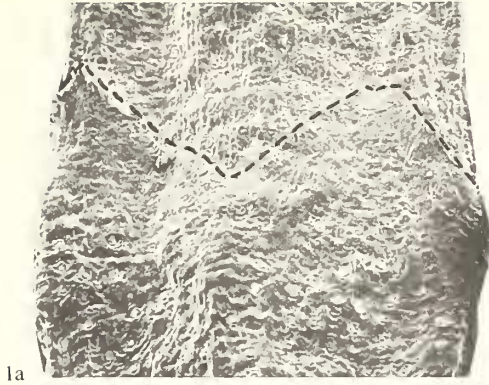
Fig. 1a, b. Two sides of the same node of an ultimate branch. Edges of leaves outlined by broken lines, SEM, $\times 40$.

Fig. 2. Cuticle of internode, light microscope, $\times 200$.

Fig. 3. Stoma, focused through the papillae in the throat of the stomatal pit, light microscope, $\times 800$.

Fig. 4. Edge of leaf, showing short hairs extending from the marginal cells, SEM, $\times 400$.

Fig. 5. Inside of internode cuticle, SEM, $\times 200$.



frequently absent in preparations, so that the inside view shows the papillae (Pl. 42, fig. 4). As seen in outer surface view (Pl. 42, fig. 1), the canopy is delimited peripherally by a circular groove, and it is the outer side of the groove which is delimited by the ring of surrounding epidermal cells. This interpretation of the stoma is supported by the appearance of specimens such as that shown in Plate 42, fig. 2 where the anti-clinal walls of the epidermis are marked by furrows; clearly here the stoma has five subsidiary cells and six surrounding epidermal cells.

No satisfactory preparations were produced of the adaxial leaf and sheath cuticle, which is delicate, but the adaxial surface appears somewhat papillate and without stomata.

Discussion and comparison. This Cenomanian species is well distinguished from the other Portuguese species. I identify it with the species described from Czechoslovakia now known as *Frenelopsis alata* (for references, see synonymy). Dr. Hlušík has kindly examined photographs of the Portuguese material and agrees that there is a very close resemblance to that recently studied by him (pers. comm.), and with which he has found male cones containing *Classopollis* in association (Hlušík and Konzalová 1976).

It seems to me from the available descriptions (Zeiller 1882; Carpentier 1937) that the specimens described from Bagnols (Turonian) in the south of France may also belong to the same species. These were described by Zeiller as *F. hoheneggeri* (Ettingshausen) and the cuticle was examined further by Carpentier when he described other specimens, again under the name *F. hoheneggeri*, from the Campanian of Sainte-Baume, France. These younger specimens, however, I do not believe are the same, but may be much closer to *F. oligostomata* from Portugal.

The material described by Broutin and Pons (1975) from the Cenomanian of Le Brouillard, France, may also represent *F. alata*, but the form of the stoma is not quite clear from the description so far published.

Frenelopsis oligostomata Romariz

Plate 43, figs. 1-6; text-fig. 2A-D

- 1900 *Frenelopsis occidentalis* Heer: Lima, p. 11 (record only).
 1937 ?*Frenelopsis hoheneggeri* (Ettingshausen): Carpentier, p. 5; pl. 1, figs. 1-5; pl. 2, figs. 1-3.
 1946 *Frenelopsis oligostomata* Romariz, p. 144; pl. 5, figs. 1, 2.
 1946 *Frenelopsis* aff. *hoheneggeri* (Ettingshausen): Teixeira, p. 236; pl. 1, figs. 1-4; pl. 2, figs. 1, 2; pl. 3, figs. 1, 2.
 1975 *Frenelopsis* (from Esgueira), Broutin and Pons, p. 10, pls. 1-4 (specimens from Esgueira).

EXPLANATION OF PLATE 42

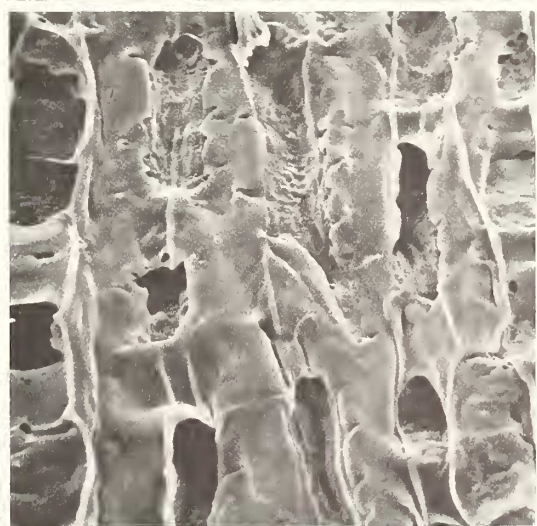
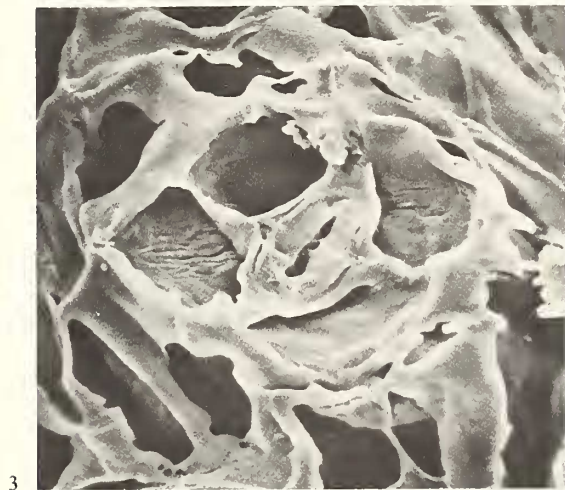
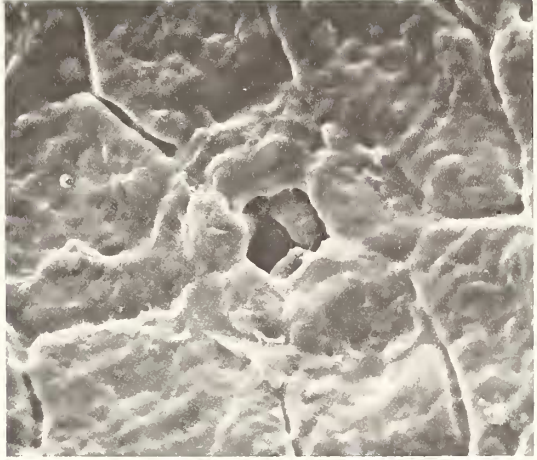
Frenelopsis alata (K. Feistmantel) Knobloch, from Nazaré (Cenomanian).

Figs. 1, 2. Stomata from opposite sides of the same branch segment, SEM, $\times 950$.

Figs. 3, 4. Stomata seen from inside cuticle. Guard cells are absent in fig. 4 and the papillae in the throat of the stomatal pit can be seen, SEM, $\times 900$.

Fig. 5. Vertical section through stomatal pit showing, at top, part of the 'canopy' and mid-way down, three of the throat papillae, two in section and one at the back, SEM, $\times 1600$.

Fig. 6. Abaxial cuticle of leaf showing cutinized hypodermis, SEM, $\times 900$.



ALVIN, *Frenelopsis*

Locality. Esgueira, near Aveiro, Beira Littorale, Portugal.

Horizon. Senonian.

Emended diagnosis. Branching (?penultimate) shoots up to 5 mm wide, somewhat zigzag. Lateral branches (?ultimate) up to 4 mm wide, arising one at each node of the parent shoot at about 30° (disregarding zigzag). Leaves in whorls of three.

Cuticle of internode about 30 μm in total thickness (measured in folds under the light microscope) with the outer periclinal wall of the epidermis about 10 μm . Epidermal cells clearly marked (Pl. 43, figs. 3, 5), mostly isodiametric but rather variable in shape and size (20–45 μm), seldom longer than wide, more frequently wider than long; longitudinal rows not well defined, except for short chains of cells. Anticlinal walls about 8 μm thick. Hypodermis of isodiametric cells sometimes present.

Stomata about the same optical density as the rest of the cuticle (Pl. 43, fig. 5); arranged in longitudinal rows, but rows somewhat obscure due to rather distant spacing of stomata (75–250 μm apart) within the rows (Pl. 43, figs. 3, 5). Subsidiary cells (four) five (or six). Mouth of stomatal pit bounded by a thick, obscurely lobed, wrinkled ring (Pl. 43, fig. 1), the number of lobes equalling the number of subsidiary cells. Papillae in the throat of the pit short, wide, and frequently obscured by a deposit of an opaque, granular substance. Subsidiary cells inconspicuous in the light microscope, but seen clearly from the inside by SEM as wide, convex cells showing faint radial striations (Pl. 43, fig. 4), the convexity corresponding to a thickening of the cuticle of the surrounding epidermal cells just beyond the outermost limit of the raised external ring; the furrow between the ring and the thickened area showing as a light translucent ring in the light microscope (Pl. 43, fig. 6). Guard cells thinly cutinized, only the parts adjacent to the subsidiary cells generally surviving maceration (Pl. 43, fig. 4). Stomatal orientation most frequently transverse.

Stomata present on the lower part of the internode covered by the leaf-sheath of the node below but, at the top of the internode, ceasing rapidly on the sheath; upper part of sheath and leaves therefore probably non-photosynthetic. Sheath and leaf margins fringed with small unicellular hairs extending from the marginal cells (Pl. 43, fig. 2).

Further description and discussion. Of the three specimens all from the same locality, one is well preserved with a cuticle, the others being only impressions. The good

EXPLANATION OF PLATE 43

Frenelopsis oligostomata Romariz, from Esgueira (Senonian).

Fig. 1. Stoma from outside, SEM, $\times 1600$.

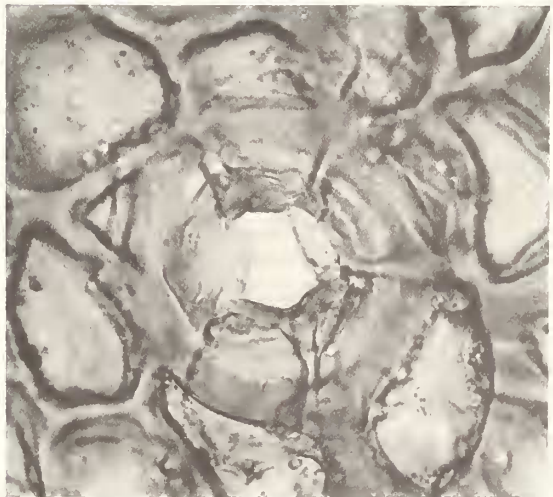
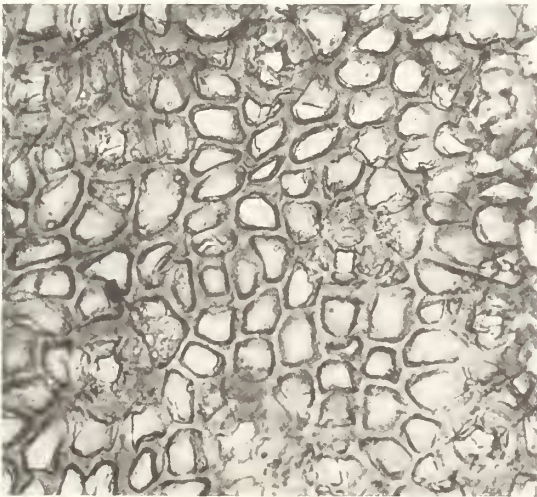
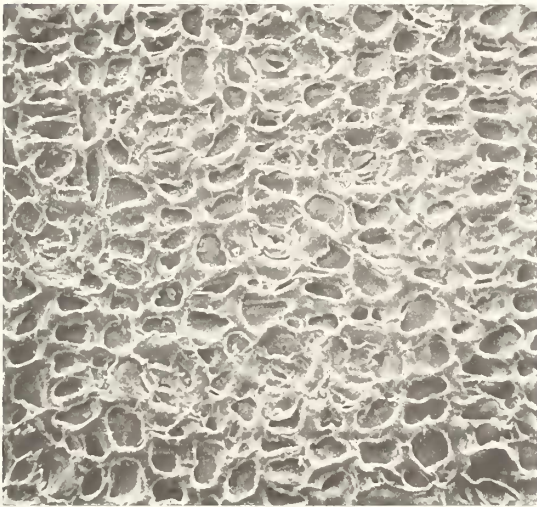
Fig. 2. Edge of leaf sheath (below) overlapping internode (above), SEM, 450.

Fig. 3. Inside of internode cuticle, SEM, $\times 180$.

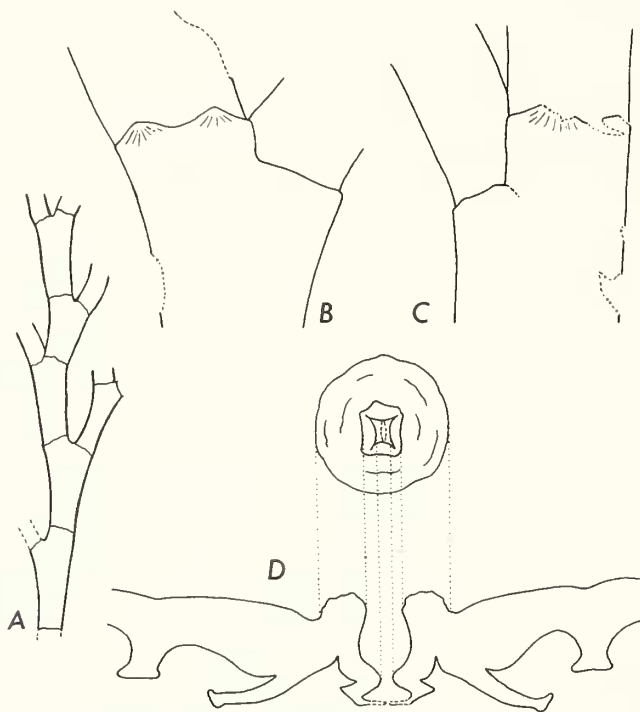
Fig. 4. Stoma seen from inside cuticle, SEM, $\times 800$.

Fig. 5. Internode cuticle, light microscope, $\times 200$.

Fig. 6. Stoma, focused through the stomatal pit, light microscope, $\times 800$.



specimen, used here for cuticle characters and figured in text-fig. 2A-C, was figured by Teixeira (1946) as his plate 1, fig. 1, but not by Romariz, though he probably used this specimen for his cuticle studies. Brontin and Pons (1975) have recently described some new specimens from Esgueira which they have not yet specifically identified. However, it is clear from their description that they represent this species.



TEXT-FIG. 2. *Frenelopsis oligostomata* Romariz. A, outline drawing of specimen. [Part of that figured by Teixeira (1946, pl. 1, fig. 1).] B, C, two successive nodes from the same specimen, $\times 25$. D, reconstruction of outside view of stoma and section of cuticle, $\times 500$.

It was not possible to be quite certain about the number of leaves at the node on the basis of the specimens in Lisbon, but the specimens of Brontin and Pons (1975) make it quite clear that there are three. Text-fig. 2B, C represents two successive nodes. Two short, triangular, striated extensions to the sheath are seen on one side of the specimen at one node (text-fig. 2B), but only one at the next (text-fig. 2C). The relationship of the branch emission to the leaves and sheath is not clear. As text-fig. 2B, C shows, the branch joins the stem at about 1 mm below the level of the top of the sheath. If the branch is axillary, then the sheath must either be attached to the main stem at the level of the branch base and then split by the growing branch, or else it may be attached rather higher but along a line which dips strongly at the subtending leaf.

The stomata, though different in a number of details from those of *F. alata*, are basically comparable (cf. text-figs. 1A and 2D). Their comparative obscurity in the light microscope (Pl. 43, fig. 5) contrasts markedly with their prominence in *F. alata* (Pl. 41, fig. 2). The granular deposit in the stomatal pit was noted by Romariz; it may represent preserved wax.

No satisfactory preparations have been made of the adaxial leaf and sheath cuticles.

No specimens of *Frenelopsis* described from elsewhere can be said to be identical to this species, with the possible exception of those reported from the Campanian of Sainte-Baume, France, by Carpentier (1937). Unfortunately, however, Carpentier's specimens are not very fully described. The epidermal cells are similar in size, shape, and arrangement and in the thickness of the anticlinal walls, but the stomata, the pits of which are blackened by a dark deposit, show few details.

The specimens tentatively named '*F. aff. alata*' by Hlušík (1974) from the Senonian of Czechoslovakia are much more like *F. alata* than *F. oligostomata*.

Genus MANICA Watson

Manica parceramosa (Fontaine) Watson

Plate 44, figs. 1-8; text-fig. 3

- 1889 *Frenelopsis parceramosa* Fontaine, p. 218; pl. 111, figs. 1-5; pl. 112, figs. 1-5; pl. 168, fig. 1.
 1946 (*pro parte*) *Frenelopsis hoheneggeri* (Ettingshausen): Romariz, p. 143; pl. 2, figs. 1, 2; pl. 3, fig. 1.
 1948 *Frenelopsis hoheneggeri* (Ettingshausen): Teixeira, p. 65; pl. 24, figs. 1-3.
 1965 (*pro parte*) *Frenelopsis hoheneggeri* (Ettingshausen): Reymanówna, p. 19; pl. 1, figs. 1, 3, 6; text-fig. 2A, C, E-M.
 1974 *Manica parceramosa* (Fontaine) Watson, p. 428. (Name only.)

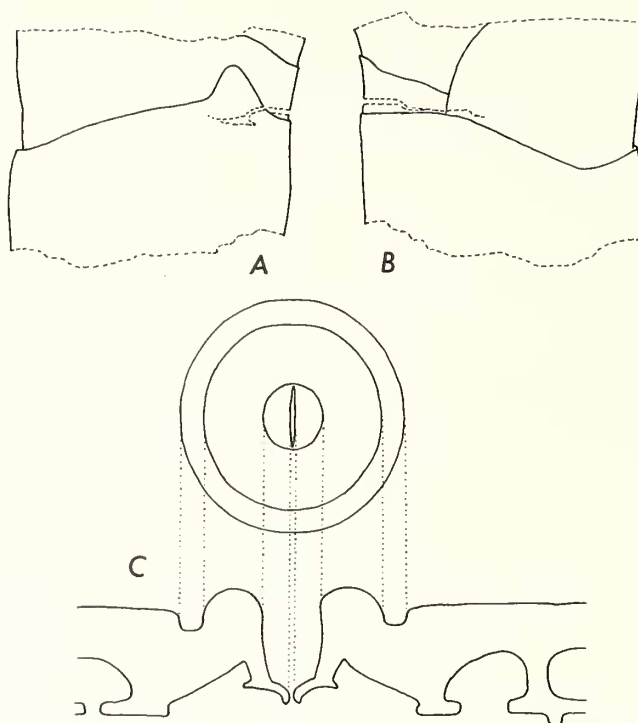
Locality. Olhos Amarelos, near Cabo da Serra, Obidos, Estremadura, Portugal.

Horizon. Aptian-Albian.

Description. Two good blocks exist in the Lisbon collection; one of them was figured by Teixeira (1946) and it is this which I have used in my study. Both blocks bear several short lengths of broken shoots and numerous isolated segments. The shoot segments are 8-10 mm wide and up to about twice as long as wide. At the node is a single, triangular leaf represented by an extension of about 0.8 mm high from the normally continuous, collar-like sheath (text-fig. 3A). Opposite the leaf (text-fig. 3B) the sheath dips to its lowest point, forming a usually shallow sulcus. Occasionally, however, as in the segment above in this same specimen, the sulcus dips right down to the node below so that the sheath is 'open' rather than 'closed'. The leaves are spirally arranged. Branching has not been clearly observed.

The flanks of the leaf and the sheath bear abundant unicellular hairs extending from the marginal cells (Pl. 44, fig. 2).

The internode cuticle is about 30 μm in total thickness (measured in folds under the light microscope) with the outer periclinal wall of the epidermis about 13 μm thick.



TEXT-FIG. 3. *Manica parceramosa* Fontaine. A, B, opposite sides of the same shoot fragment showing parts of two internodes, $\times 6$. C, reconstruction of outside view of stoma and section of cuticle, $\times 500$ approx.

The epidermal cells are clearly seen in the light microscope (Pl. 44, figs. 7, 8) but owing to often strong cutinization of the inner periclinal wall and part of the hypodermis, they are not always clear in the SEM view of the inner surface (Pl. 44, fig. 6). The epidermal cells are more or less isodiametric, but usually elongated (up to twice as long as wide) between the stomatal rows; they are $10\text{--}20\ \mu\text{m}$ wide. The anticlinal walls are about $6\ \mu\text{m}$ thick. Hypodermal cells are most strongly cutinized between the stomatal rows; they are elongated, about $10\ \mu\text{m}$ wide, and marked by thin flanges underlying the epidermal cuticle (Pl. 44, fig. 6).

EXPLANATION OF PLATE 44

Manica parceramosa (Fontaine) Watson, from Olhos Amarelos (Aptian-Albian).

Fig. 1. Internode cuticle from outside showing four stomata, SEM, $\times 420$.

Fig. 2. Edge of leaf-sheath, showing rather long hairs extending from the marginal cells, SEM, $\times 800$.

Fig. 3. Outer surface of adaxial leaf cuticle, SEM, $\times 400$.

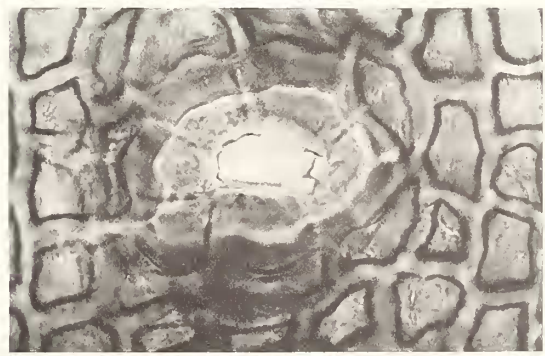
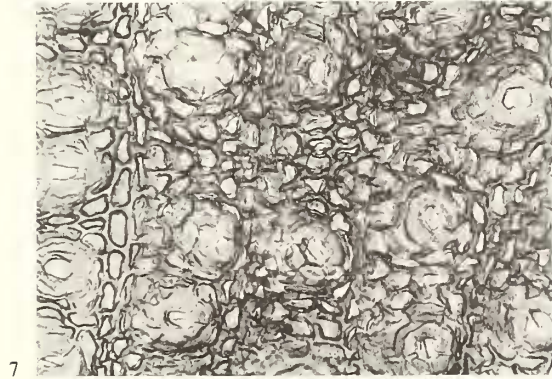
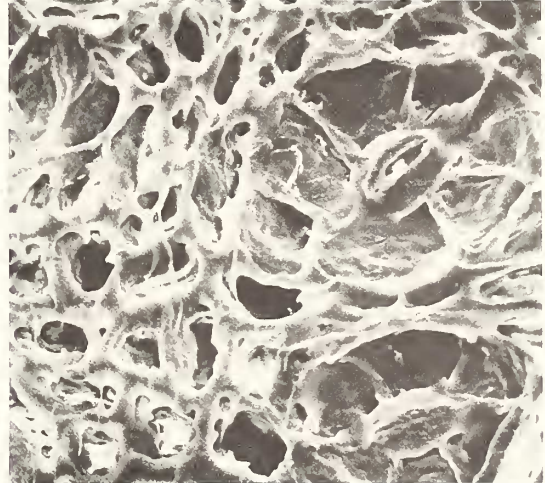
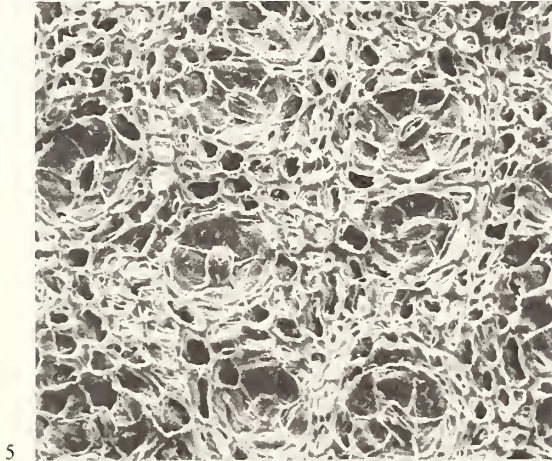
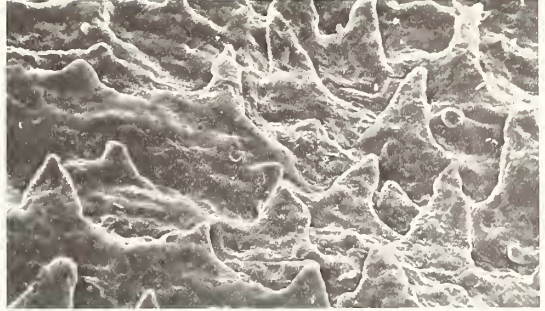
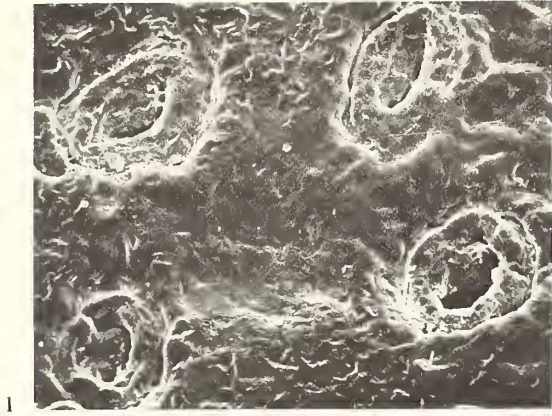
Fig. 4. Inner surface of adaxial leaf cuticle, SEM, $\times 400$.

Fig. 5. Internode cuticle from inside, SEM, $\times 220$.

Fig. 6. Internode cuticle from inside showing two stomata and cutinized hypodermis. Stomata showing ring of subsidiary cells and guard cells, SEM, $\times 550$.

Fig. 7. Internode cuticle, light microscope, $\times 150$.

Fig. 8. Stoma, focused through stomatal pit, light microscope, $\times 600$.



The stomata appear optically less dense than the rest of the epidermis and are therefore conspicuous in the light microscope. They are in well-defined rows separated by two to four epidermal cells.

There are (four), five to six (or seven) subsidiary cells forming the stomatal pit. Externally (Pl. 44, fig. 1), the pit is seen to be bounded by a thick raised ring which is in turn separated from the rest of the epidermis by a fairly deep furrow; again here it is the outer limit of this furrow which is formed by the edges of the surrounding epidermal cells of which there are usually one or two more than the number of subsidiary cells. In the light microscope (Pl. 44, fig. 8) the furrow is indicated by the narrow light band just inside the dense ring formed by the surrounding epidermal cells. The guard cell cuticles are fairly thick and therefore generally present in preparations; orientation is random.

Stomata fade out towards the edge of the leaf-sheath and are absent from the leaf itself, the outer surface of which is papillate due to protruding epidermal cells. The adaxial surface of leaf and sheath is strongly papillate (Pl. 44, fig. 3). The adaxial cuticle of the leaf consists of almost square cells, the regular arrangement of which is sometimes disturbed by a ring-like group of cells suggestive of an abortive stoma (Pl. 44, fig. 3, top left). In the sheath, the adaxial cuticle shows a continuous hypodermis.

Discussion and comparison. Specimens belonging to this species may possibly have been included by Schenk (1869) in the material described as *F. hoheneggeri* from the Carpathians. Some of his specimens (e.g. Schenk, pl. 4, figs. 5–7) certainly bear a resemblance to this species. As already stated above and by Reymanówna (1965) and Hlušík (1974), the status of *F. hoheneggeri* is uncertain. However, most of Schenk's specimens appear to be of a kind having more elongated segments with more than one leaf at the node, possibly three. The material described by Remanówna was certainly mixed. Dr. Reymanówna and I have recently re-examined this material and find that the shoots with more elongated segments and with three leaves show certain cuticle differences from those with shorter segments and only one leaf. These latter, on which Remanówna's (1965) description of the cuticle was based, are regarded as identical to the Portuguese specimens described here and also to material from the Wealden of England which Dr. Watson and I are at present investigating. Dr. Watson has recently re-examined Fontaine's type material of

EXPLANATION OF PLATE 45

?*Frenelopsis occidentalis* Heer, from Almagem (Aptian-Albian).

Fig. 1. Internode cuticle from outside, SEM, $\times 170$.

Fig. 2. Single stoma from outside, showing polygonal mouth of the stomatal pit and papillae in throat, SEM, $\times 1100$.

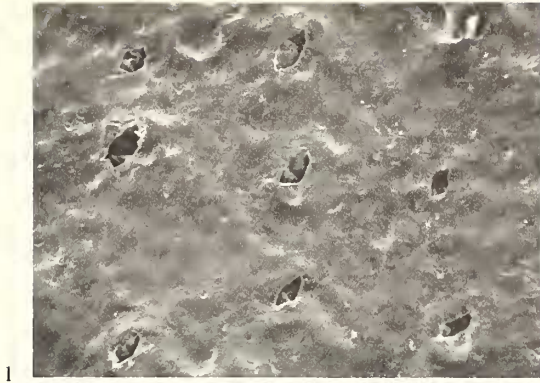
Fig. 3. Internode cuticle from inside, SEM, $\times 170$.

Fig. 4. Stoma from inside, showing subsidiary cells with entrances to the hollow throat papillae, SEM, $\times 800$.

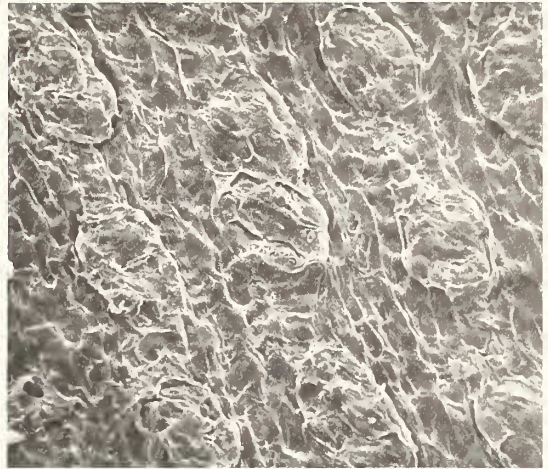
Fig. 5. Section of stoma. Cuticle somewhat compressed, SEM, $\times 1400$.

Fig. 6. Internode cuticle, light microscope, $\times 200$.

Fig. 7. Stoma, focused through stomatal pit showing the prominent throat papillae, light microscope, $\times 800$.



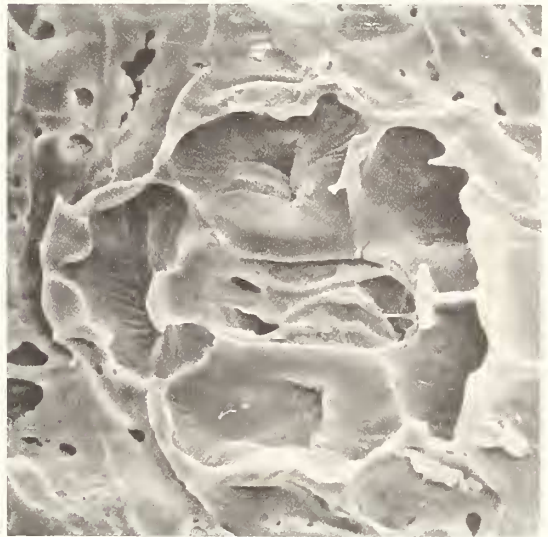
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3



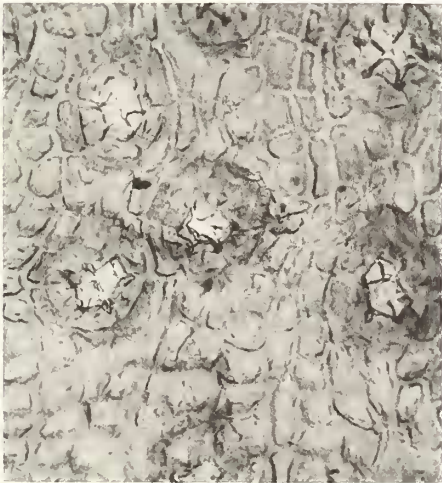
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4



5



6



7

ALVIN, ?*Frenelopsis*

F. parceramosa in the Smithsonian Institution and has concluded that it is identical to the English material. She will shortly publish an emended diagnosis of the species.

Variations, however, do occur. The variation within the Portuguese material in the 'open' or 'closed' nature of the leaf-sheath has also been noted by Watson (1964) in material from England. No papillae have been observed extending from the raised ring around the mouth of the stomatal pit in the Portuguese specimens (though the cuticles of only two individual segments have been examined). Papillae are generally present in material from elsewhere, though they may be absent from some English material.

Watson (1974) has proposed the name *Manica* for *Frenelopsis*-like conifers with spirally arranged leaves. Certainly, among modern conifers, such a difference would be regarded as fundamental and meriting generic distinction. Accordingly, I am, for the present, using this name. However, the resemblances in morphology and cuticle characters among these fossil conifers, regardless of phyllotaxy, are strong and when more information concerning the other parts of the plants becomes available, it is possible that the difference in phyllotaxy may no longer provide sufficient grounds for generic separation.

Oishi (1940) recorded this species from Korea, but his records cannot be accepted on the basis of his description which gives no anatomical detail.

Genus ?*Frenelopsis* Schenk
? *Frenelopsis occidentalis* Heer

1881 *Frenelopsis occidentalis* Heer, p. 21; pl. 12, figs. 3b, 4-7.

1946 (*pro parte*) *Frenelopsis hoheneggeri* (Ettingshausen): Romariz, p. 143; pl. 1, figs. 1-3.

1948 *Frenelopsis hoheneggeri* (Ettingshausen): Teixeira, p. 55; pl. 14, fig. 4.

Locality. Vale de Almargem, between Vale de Figuera and Rio de Sapos, near Almargem, Estremadura, Portugal.

Horizon. Aptian-Albian.

Emended diagnosis. Branching segmented shoots up to 4 mm broad. Segments up to four times longer than broad.

Cuticle of internode up to 60 μm in total thickness with the outer periclinal walls of the epidermis about 25 μm thick. Inner periclinal walls almost continuously cutinized except for small perforations (Pl. 45, figs. 3, 4). Anticlinal walls of hypodermis slightly cutinized.

Epidermal cells in longitudinal rows, isodiametric or up to twice as long as wide, 15-25 μm wide with anticlinal walls about 6 μm thick.

Stomata arranged in longitudinal rows and optically slightly denser than the rest of the epidermis (Pl. 45, fig. 6). Subsidiary cells, five to six. As seen from the outside (Pl. 45, fig. 1), mouth of stomatal pits flush with general cuticle surface or slightly raised. Pit mouth irregularly polygonal in shape, the number of sides equalling the number of subsidiary cells. Papillae in the throat of the pit equalling the number of subsidiary cells, massive and obscuring the guard cells from above (Pl. 45, figs. 2, 5). Guard-cell cuticles rather thin, but commonly surviving maceration. Stomata irregularly orientated, but with some tendency to be parallel in a given area of cuticle.

Further description and discussion. Heer (1881) originally described his material as coming from a different locality (Vale de Lobos) but Choffat (1894) gave reason for believing that it was from Almargem. This was accepted by Teixeira (1948) and Romariz (1946) who regarded the material as Heer's holotype of *F. occidentalis*. I therefore use this name. The single block apparently representing Heer's holotype bears a number of broken shoots and isolated segments. Much of the compressed material has peeled off leaving only impressions. Unfortunately it has not been possible to determine the leaf arrangement and for this reason the generic name must be regarded as tentative.

The specimen, together with those from Olhos Amerelos which I have identified as *Manica parceramosa*, was identified as *F. hoheneggeri* (Ettingshausen) by Romariz. However, although the material from Almargem is fragmentary and has not allowed a very full description, the cuticle is well preserved and provides evidence that it is probably distinct. The most notable differences are the much greater thickness of the cuticle, the more strongly cutinized hypodermis, and stomata differing in a number of details. I know of no other species of *Frenelopsis* with a similar cuticle but the form described as '*Frenelopsis* sp.' by Hluštik (1974) from Štramberk (?Hauterivian) shows some resemblance.

Other records from Portugal. Teixeira (1948) records *Frenelopsis* from several other Cretaceous localities. Some of these specimens I was able to examine in Lisbon, but in none is the preservation good enough for cuticle preparations and accurate identification. *F. leptoclada* Saporta (1894) from the Aptian of Caixaria and also from the Valanginian of San Sebastian in Spain, is based on poor impressions only and cannot therefore be characterized in any worthwhile way.

Another species, probably new, having two opposite leaves at each node, from Sesimbra (Hauterivian or Barremian) is currently being investigated by Dr. J. Pais, University of Lisbon.

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K. L. ALVIN

Department of Botany
Imperial College of Science and Technology
Prince Consort Road
London SW7 2BB

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